Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 51, No. 2, June 2022
pages (224-238)

sciendo

ISSN 1730-413X
eISSN 1897-3191

Biodiversity of the benthic diatom flora in the coastal zone of the Gulf of Gdańsk: a case study of the Gdynia–Sopot transect

by

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DOI: **https://doi.org/10.26881/oahs-2022.2.10**
Category: **Original research paper**
Received: **November 4, 2021**
Accepted: **April 20, 2022**

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Abstract

The objective of this study is to determine microhabitat preferences of benthic species occurring in epilithic (living on stones), epipsammic (growing on sand), epipelic (growing on mud) and epiphytic (living on seagrass) assemblages of the shallows of the Gulf of Gdańsk (southern Baltic Sea). The study material was collected from 19 sites along the Gdynia–Sopot coastal zone, including the Port of Gdynia. Most of the identified diatom taxa were observed in two or three microhabitats. However, diatom species living in only one type of microhabitat and those occurring in all analyzed microhabitats were also recorded. Autecological preferences of the identified diatoms indicate organic pollution of the coastal zone of Gdynia and Sopot. However, a higher frequency of α-mesosaprobionts and polysaprobionts indicates an increase in organic pollution in the Port of Gdynia and Marina Sopot, which is associated with intense port activity and large tourist traffic.

Key words: benthic diatoms, microhabitat, ecology, coastal zone, Gulf of Gdańsk, Baltic Sea

1. Introduction

Diatom research has been conducted in the Gulf of Gdańsk for nearly 100 years. The first researcher to document the occurrence of diatoms in the bay area was Schulz (1926). The modern and fossil diatom flora of the Gulf of Gdańsk was described by, among others, Rumek (1948), Pliński (1987, 1988, 1990, 1995), Witkowski (1994), Witkowski & Pempkowiak (1995), Pliński & Kwiatkowski (1996), Stachura & Witkowski (1997), Witak (2000, 2002, 2010, 2013), Bogaczewicz-Adamczak et al. (2001), Witak et al. (2006, 2011), Witak & Dunder (2007), Leśniewska & Witak (2008, 2011), Pliński & Witkowski (2009, 2011, 2013a,b), Witak & Pędziński (2018), Pędziński & Witak (2019). Previous studies usually focused on diatoms preserved in the sediments in different parts of the Gulf of Gdańsk. The diatom research in the coastal zone of the Gulf of Gdańsk was used to determine the degree of water organic pollution (Bogaczewicz-Adamczak et al. 2001; Zgrundo & Bogaczewicz-Adamczak 2004) and to investigate diatom preferences with respect to habitat (Witak et al. 2020). An important aspect of many diatom studies is to determine the degree of anthropogenic eutrophication. A multifaceted discussion on the relationship between diatoms and eutrophication in the Gulf of Gdańsk was included in the works of Witkowski (1994), Stachura & Witkowski (1997), Witak (2010, 2013), Leśniewska & Witak (2011), Witak & Pędziński (2018) and Pędziński & Witak (2019). Consequently, the so-called anthropogenic assemblage dominated by small planktic diatoms tolerating high levels of nitrogen, phosphorous and organic matter was defined, represented by *Cyclotella meneghiniana* Kützing, *C. atomus* Hustedt, *C. choctawhatcheeana* (Prasad in Prasad) Neinow & Livingston and *Thalassiosira levanderi* Van Goor (Witkowski 1994; Witak 2010, 2013; Witak & Pędziński 2018; Pędziński & Witak 2019). In addition, *Catenula adhaerens* (Mereschkowsky) Mereschkowsky, *Cocconeis neothumensis* Krammer, *Fragilaria atomus* Hustedt, *Gedaniella guenter-grasii* (Witkowski et Lange-Bertalot) Li, Sato & Witkowski and *Pseudostaurosira brevistriata* (Grunow) Williams & Round are frequently observed among the benthic species in eutrophic waters (Leśniewska & Witak 2008, 2011; Witak 2010, 2013).

The latest research on species diversity of epilithon, epipsammon and epiphyton was conducted in the inner coastal zone of the Hel Peninsula (Witak et al. 2020). That study has shown that diatom taphocoenoses are represented by species that prefer one type of microhabitat: epilithon is characterized by the presence of *Denticula creticola* (Østrup) Lange-Bertalot & Krammer and *Diatoma tenuis* C. Agardh, the epipsammic community contained *Catenula adhaerens* and *Navicula germanopolonica* Witkowski & Lange-Bertalot, while epiphyton was represented by *Cocconeis pediculus* Ehrenberg, *Gomphonema olivaceum* (Hornemann) Ehrenberg and *Mastogloia pumila* (Grunow) Cleve. The study has also shown that some species, despite being assigned to a specific microhabitat in the literature, can also be present in large numbers in various types of microhabitats. Such species include, among others, *Halamphora coffeaeformis* (C. Agardh) Mereschkowsky, *Nitzschia frustulum* (Kützing) Grunow, *Rhoicosphaenia abbreviata* (C. Agardh) Lange-Bertalot and *Tabularia fasciculata* (C. Agardh) Williams & Round. Despite many years of research on diatoms in the coastal zone of the Gulf of Gdańsk, knowledge about the relationship between the species composition of benthic diatoms and microhabitats requires further investigation. It is necessary to obtain microhabitat data for diatom taxa. The current global warming will be the cause of rising water levels in the world ocean. It will also cause sediment facies changes in the coastal zone. The past climatic changes have been recorded in the postglacial sediments of the Gulf of Gdańsk. Holocene climate fluctuations have resulted in the development of subsequent phases of the Baltic Sea evolution, evident also in the Gulf of Gdańsk. Diatoms, being sensitive to numerous environmental factors, are excellent bioindicators of Holocene salinity changes. The early Holocene decrease in salinity during the Ancylus Lake stage has resulted in a higher frequency of freshwater species (Witak et al. 2006; Witak & Jankowska 2014). The middle Holocene marine transgression in the initial phase of the Littorina Sea stage is well documented by the peak occurrence of marine planktic diatoms (Witkowski & Miller 1999; Witak et al. 2006; Leśniewska & Witak 2008; Witak 2010, 2013). The last stage of the Baltic Sea, the so called Post-Littorina Sea, is characterized by a decline in the frequency of euhalobous species (Witkowski 1994; Witak 2013). Diatoms are also great indicators of changes in the content of nutrients in water. Therefore, they testify to changes in trophic and saprobic status resulting from the inflow of river waters (Bogaczewicz-Adamczak et al. 2001; Zgrundo & Bogaczewicz-Adamczak 2004). Against the background of the well-established knowledge of changes in the structure of diatom assemblages in relation to salinity, trophic and saprobic status, information is needed on the benthic flora in relation to microhabitats. The objective of this study is to examine the taxonomic and ecological diversity of benthic diatom communities inhabiting various microhabitats in relation to environmental conditions modified by human influence.

2. Study area

The study area is located in the coastal zone of the south-western part of the Gulf of Gdańsk, the southern Baltic Sea. This region includes shallows with a depth not exceeding 30 cm b.s.l. along the shore between Gdynia and Sopot, as well as an area of deeper water in the Port of Gdynia dredged to ca. 16 m b.s.l (Fig. 1). Three types of coasts occur in the area, i.e. accumulative, cliffs and anthropogenic. The northern section represents the anthropogenic coast and comprises the Port of Gdynia and the Seaside Boulevard with a concrete revetment. The central part of the analyzed fragment of the coastal zone has the form of a cliff. This part of the shore is exposed to the intense erosive action of waves, which results in the presence of the Orłowo Cliff with the most seaward jutting Orłowo Headland, which constitutes a conventional border between Puck Bay and the open part of the Gulf of Gdańsk. To the south, the cliff is cut off by the Kacza River. This part of the shore features anthropogenic elements in the form of hydrotechnical structures, i.e. a pier and spurs. The southern part, located between the mouth of the Kolibianka River and the mouth of the Vistula River outside the city of Gdańsk, has an accumulative character. In the Sopot area there is a wide sand beach. Nevertheless, hydrotechnical structures such as the pier and spurs largely affect the hydrodynamics of this part of the bay (Basiński et al. 1993).

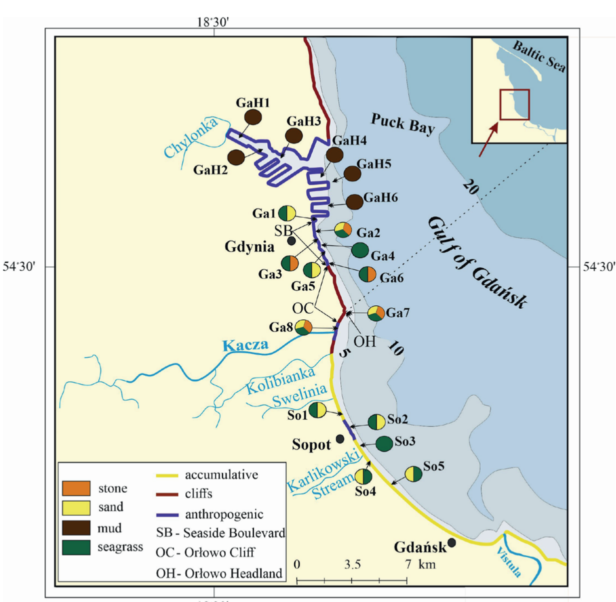

Figure 1

Location of the study area

The hydrological regime of the coastal zone of the Gulf of Gdańsk is determined by shallow water depth, climatic conditions, and the inflow of saline waters from the open sea. In addition, freshwater discharge from the surrounding land is an important factor influencing the hydrology of the study area. The deeper part of the Gulf of Gdańsk is controlled by the strong runoff from the Vistula mouth (Kravtsov et al. 2002). The influence of the Vistula River in the coast between Gdynia and Sopot is strongly limited due to prevailing winds blowing from the W, WNW and WSW directions, which distribute river water in an easterly direction. On the other hand, winds blowing from the E, ENE and ESE directions cause the Vistula runoff to move westward. The impact of the Vistula waters in the study area increases during extreme floods when the flood wave can reach up to 27 km from the mouth of the Vistula (Wielgat-Rychert et al. 2013). Moreover, the waters of the Vistula have the greatest impact on the nutrient load in the Gulf of Gdańsk. They introduce 90% of nitrogen and 81% of phosphorus (Andurlewicz & Witek 2002). However, the content of nutrients in the coastal zone of the Gulf of Gdańsk is significantly affected by industry (0.3% N, 0.9% P) and wastewater treatment plants (3% N, 3% P; Andurlewicz & Witek 2002). The impact of other rivers and streams, including the Kacza, the Chylonka, the Kolibianka, the Swelinia and the Karlikowski Stream is limited to the proximity of their outlets (Majewski 1972). The Baltic Sea monitoring studies conducted in 2010–2020 showed that the concentrations of total phosphorus and total nitrogen were lower in 2020 than in previous years (Drgas 2021).

Rivers provide warm water in summer and cool water in winter. On the other hand, seawater from the Gdańsk Basin have the opposite effect and cause temperature increase in winter and decrease in summer (Nowacki 1993a). Moreover, thermal conditions of the waters in the study area are strictly dependent on changes in air temperature in particular seasons. Long-term studies show the advantage of higher water temperatures compared to air temperature from August to January. The opposite trend is observed from March to June. Moreover, two compensations for temperature differences are noticeable. The first one occurs in February and the second one in July (Kwiecień 1990). The lowest air temperatures in the coastal zone of the south-western Gulf of Gdańsk are recorded in January and range from –1°C to –2°C, while the highest extreme values occur in August (ca. 28°C; Kwiecień 1990). At the same time, the surface water temperature reaches the lowest values in February (ca. 0°C) and the highest values in August (ca. 24°C; Herman 2021). The average water temperature in the coastal zone between Gdynia and Sopot from December to April (cold season) is 2.5–3.0°C. In the warm season, the temperature increases from 15.6–16.0°C in the vicinity of river mouths to 15.1–15.5°C in the area of the Port of Gdynia (Urbański et al. 2007). Seasonal changes in salinity are also observed. The average salinity in the cold season near the port and the Orłowo Headland is 7.59–7.75 PSU. In the coastal zone of Sopot, the salinity increases to 7.76–7.78 PSU. In the warm season, the salinity of 7.38–7.49 PSU is observed in almost all parts of the coastal zone of Gdynia and Sopot. Only in the area of the Orłowo Headland, the salinity drops to the value of 7.18–7.37 PSU due to the inflow of the Kacza River (Urbański et al. 2007).

The water circulation in the Gulf of Gdańsk is determined by the shape of the coastal zone and the frequent occurrence of winds from the western sector (Kowalik 1990). The basin is dominated by clockwise currents with an average speed of about 10 cm s^{-1} (Nowacki 1993b). The westerly winds cause the formation of currents that bring water from the outer side of the Hel Peninsula to the eastern side of the Gulf of Gdańsk. The coastal zone is characterized by the propagation of currents parallel to the shore (Kowalik 1990). There are also bottom currents, the direction of which is opposite to the surface currents and their speed is about 4 cm s^{-1} (Nowacki 1993b).

The bottom of the shallow-water zone of the Gulf of Gdańsk is mainly composed of sandy sediments (Kramarska 1995). In the Port of Gdynia, there are fine-grained sands and muds. In the marina, on the other hand, there are silty sands (Urbański et al. 2007). The remaining part of the studied coastal zone is covered with very well-sorted fine-grained sand. Less sorted sediments, represented by coarse sand, gravel and stones, occur only in the area of the Orłowo Cliff (Majewski 1990). The content of organic matter in sandy sediments is low and does not exceed 1%. However, in the mouth of the Kacza River, it increases to 5% (Majewski 1990).

The flora near the seabed of the coastal zone of the Gulf of Gdańsk is not rich and usually occurs to a depth of 8 m (Ringer 1990). However, high biodiversity is typical of the shallow-water region along a coastal cliff moraine plateau called Kępa Redłowska, where 17 species of macroalgae were identified (Pliński & Florczyk 1993). Numerous species of red algae – *Ceramium diaphanum* (Lightfoot) Roth, *Furcellaria lumbricalis* (Hudson) Lamouroux, green algae – *Cladophora* sp. Kützing and brown algae – *Sphacellaria radicans* (Dillwyn) C. Agardh have been observed in this area (Kruk-Dowgiałło et al. 2009). A valuable macroalga occurring along Kępa Redłowska is *Zostera marina* Linnaeus, which is the only species of seagrass observed in the Baltic Sea. This species is often found in the northern part of Puck Bay along the Hel Peninsula (Kruk-Dowgiałło & Opioła 2001; Witak et al. 2020). Until the late 1950s, *Zostera marina* was an important component of the underwater meadows. Since the late 1960s, a gradual decline of this species has been observed. However, studies conducted at the turn of the 20th and 21st centuries indicate a gradual recovery of the *Zostera marina* population in Puck Bay (Jankowska 2017).

3. Materials and methods

The material studied was collected in July 2016 along the coastal zone of the Gulf of Gdańsk from the Port of Gdynia up to the city limits of Sopot. A total of 19 sites were surveyed, including six sites in the Port of Gdynia (sites GaH1–6), eight sites along the coastal zone of Gdynia (sites Ga1–8) and five sites along the coastal zone of Sopot (sites So1–5; Fig. 1). Four samples were collected at site Ga2 (Ga2a,b,c,d), and two samples each were collected at sites Ga3 (Ga3a,b) and So1 (So1a,b; Table 1). At most sites, the diatom flora was analyzed from several microhabitats. At five sites (Ga2–3, Ga6–8), the study material was collected from stones. Sand was collected at five sites in Gdynia (Ga1–2, Ga5, Ga7–8) and four sites in Sopot (So1–2, So4–5). Muddy sediments were collected only in the Port of Gdynia (GaH1–6). Seagrasses were collected at 13 sites (Ga1–8, So1–5). A total of 37 samples were analyzed.

Diatom samples containing live cells were prepared according to the standard procedure of Battarbee (1986). All samples were treated with 30% H_2O_2 to remove organic matter. However, sediment samples (ca. 0.5–1 g of dry sediment) were previously treated with 10% HCl to remove calcium carbonate. Quantitative diatom analysis was carried out on all samples. Moreover, qualitative analysis was performed on sandy and muddy sediments. The random settling technique was used to estimate the concentration of diatom valves per unit weight of dry sediment (Bodén 1991). Permanent diatom preparations were mounted in Naphrax with a refractive index n_D of 1.73. The analysis was performed under a Nikon ECLIPSE E200 light microscope at a magnification of ×100, using oil immersion. Only whole, undamaged diatom valves were considered for counting. The counting method of Schrader and Gersonde (1978) was applied, and ca. 300–500 valves in each sample were counted to estimate relative abundance of each taxon. Row counts were converted into relative abundance of

Table 1

Characteristics of the analyzed samples. Types of microhabitats: st – stone, sa – sand, mu – mud, sg – seagrass. Black dots represent single samples collected

Sites	Samples	Φ	λ	Location		Depth [m]	Types of microhabitats			
							st	sa	mu	sg
GaH1	GaH1	54°32.523N	18°30.32E	GDYNIA PORT	port channel	13.6			•	
GaH2	GaH2	54°32.30N	18°31.20E		Dock VII	15.6			•	
GaH3	GaH3	54°32.10N	18°31.85E		port channel	12.3			•	
GaH4	GaH4	54°31.85N	18°33.27E		Dock III	14.4			•	
GaH5	GaH5	54°31.70N	18°33.62E		south channel	8.7			•	
GaH6	GaH6	54°31.26N	18°33.50E		Dock I	9.2			•	
Ga1	Ga1	54°30.999N	18°33.138E	GDYNIA	beach	0.25		•		•
Ga2	Ga2a	54°30.774N	18°33.062E			0.25	•	•		•
	Ga2b									•
	Ga2c									•
	Ga2d									•
Ga3	Ga3a	54°30.573N	18°33.203E		Seaside Boulevard	0.3				•
	Ga3b						•			
Ga4	Ga4	54°30.499N	18°33.258E			0.3				•
Ga5	Ga5	54°30.333N	18°33.412E			0.3		•		•
Ga6	Ga6	54°30.147N	18°33.527E			0.3	•			•
Ga7	Ga7	54°29.101N	18°34.118E		beach	0.3	•	•		•
Ga8	Ga8	54°28.788N	18°33.834E		pier	0.2	•	•		•
So1	So1a	54°27.057N	18°34.062E	SOPOT	beach	0.3		•		•
	So1b									•
So2	So2	54°26.811N	18°34.345E		pier	0.25		•		•
So3	So3	54°26.447N	18°34.636E		beach	0.3				•
So4	So4	54°26.115N	18°35.051E			0.24		•		•
So5	So5	54°25.666N	18°35.751E			0.27		•		•

all valves counted. The following identification keys were used to identify diatoms: Hustedt (1927–1966), Krammer & Lange-Bertalot (1986, 1988, 1991a,b), Pankow (1990), Krammer (2000), Lange-Bertalot (2001), Bąk et al. (2012). In addition, the identified diatoms were classified with respect to their autoecological preferences, including microhabitat, salinity, trophic and saprobic status, which was completed based on OMNIDIA 6.08 software. All details of ecological groupings were presented by Witak et al. (2020). In the case of some marine and brackish water species, trophic and saprobic preferences are irrelevant. The percentage content of all ecological groups was estimated in each sample. Only species with frequency exceeding 3% in at least one sample were selected for diatom diagrams prepared using TILIA 2.0.37 (Grimm 2011).

4. Results

A total of 147 species, subspecies, varieties and forms belonging to 56 genera were identified in the material studied (Fig. 2). Epipelic diatoms were the most diverse group, represented by 86 species. Epilithic and epiphytic diatoms were less diverse, with 68 and 71 species identified in these groups, respectively. The lowest diversity, 68 species, was observed in the epipsammic community.

Diatom taphocoenoses of the shallow coastal zone of the Gulf of Gdańsk are usually dominated by benthic species. Planktic species constituted the allochthonous element of the studied material. The exception is muddy sediments in the Port of Gdynia, where epipelon is mainly represented by planktic species with frequency reaching 80%. This group was predominantly represented by eutraphentic diatoms, including *Thalassiosira levanderi*, *Cyclotella choctawhatcheeana* and *Stephanodiscus hantzschii* Grunow. All these species belong to the so-called anthropogenic assemblage reported by Witkowski (1994), Witak (2010, 2013), Witak & Pędziński (2018), Pędziński & Witak (2019). In the epipsammic community, plankton occurs rarely, with a higher content of *Cyclotella atomus* and *Lindavia radiosa* (Grunow) De Toni & Forti at sites Ga5 and Ga7. The lowest frequency of planktic species (up to 1%) was observed in the epilithic and epiphytic community.

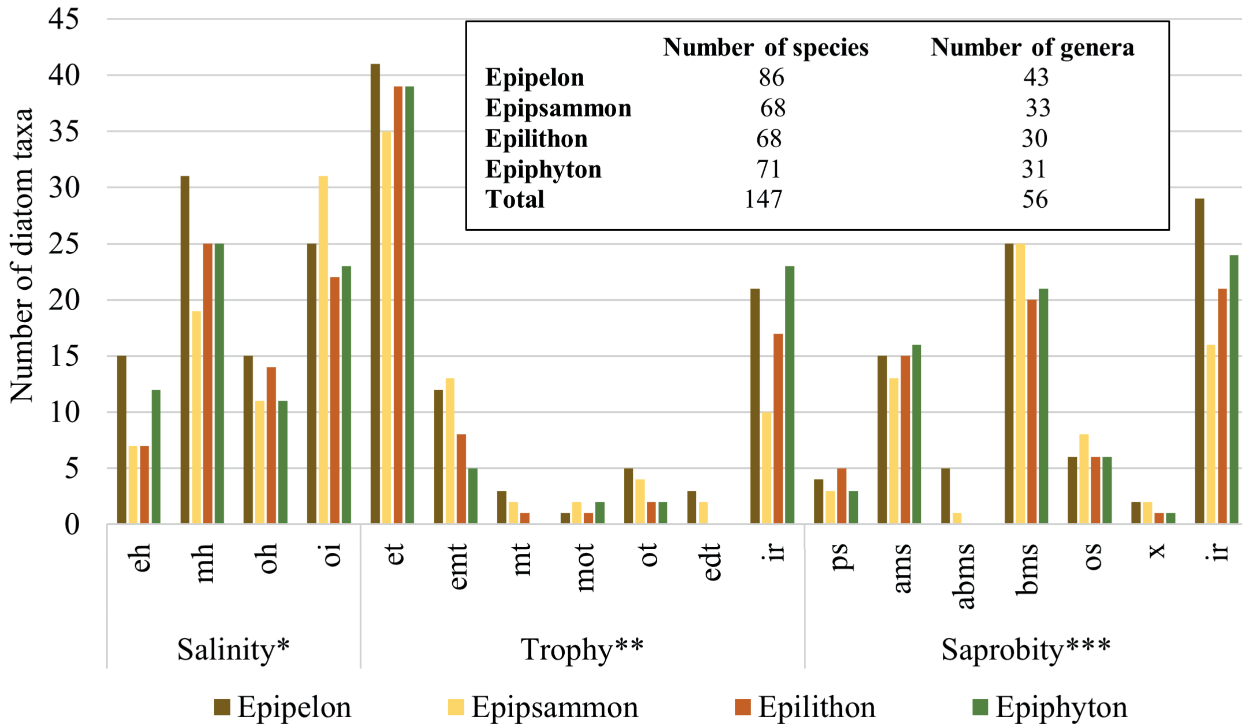

Figure 2

The number of diatom taxa (species, subspecies, varieties, forms) versus ecological preferences: *eh-euhalobous, mh-mesohalobous, oh–oligohalobous halophilous, oi–oligohalobous indifferent; **et–eutraphentic, emt–eu-mesotraphentic, mt–mesotraphentic, mot-meso-oligotraphentic, ot–oligotraphentic, edt–eurydystrophic, ir-irrelevant; ***ps–polysaprobous, ams–α-mesosaprobous, abms–α-β-mesosaprobous, bms–β-mesosaprobous, os–oligosaprobous, x-xenosaprobous, ir-irrelevant

4.1. Epilithon

In the Gdynia region, oligohalobous halophilous, eutraphentic and β-mesosaprobic diatoms predominate in the epilithon. Their frequency usually exceeds 80% (Fig. 3). However, at the mouth of the Kacza River (Ga8), the frequency of β-mesosaprobionts drops to ca. 40%. At the same time, the percentage of α-mesosaprobionts increases to ca. 40%. Diatoms growing on stones (Gdynia sites) were usually dominated by the species *Diatoma moniliformis* (Kützing) Williams, the frequency of which ranged from 19% (Ga2a) to 88% (Ga3b; Fig. 4). The α-mesosaprobic species *Rhoicosphaenia abbreviata* with a frequency of ca. 19% and the polysaprobiont *Navicula perminuta* Grunow (≤ 5%) were recorded at almost all Gdynia sites. Only at site Ga2a the frequency of *N. perminuta* did not exceed 3%. Freshwater diatoms represented by *Cocconeis pediculus*, *Epithemia sorex* Kützing, *Rhopalodia gibba* var. *gibba* (Ehrenberg) O. Müller and *R. gibba* var. *minuta* Krammer occurred sporadically. However, their percentage increases to 3–10% at site Ga2a, and they are accompanied by marine and brackish diatoms, i.e. *Bacillaria paxillifera* (O. F. Müller) Marsson, *Gedaniella mutabilis* (Grunow) Li & Witkowski, *Grammatophora marina* (Lyngbye) Kützing, *G. oceanica* Ehrenberg, *Melosira moniliformis* C. Agardh, *M. nummuloides* C. Agardh, *Tabularia fasciculata*. Moreover, at site Ga6, *Nitzschia frustulum* reaches a frequency of ca. 39%.

4.2. Epipsammon

The epipsammic assemblage of the Gdynia and Sopot zone is dominated by eutraphentic diatoms with a maximum frequency of 78% at site Ga8 (Fig. 3). They were accompanied by eu-mesotraphentic species (7–35%). The percentage of saline groups indicates a slightly higher frequency of mesohalobous diatoms at the Sopot sites than in Gdynia. The brackish species *Planothidium delicatulum* (Kützing) Round & Bukhtiyarova (Fig. 4), belonging to eutraphents and

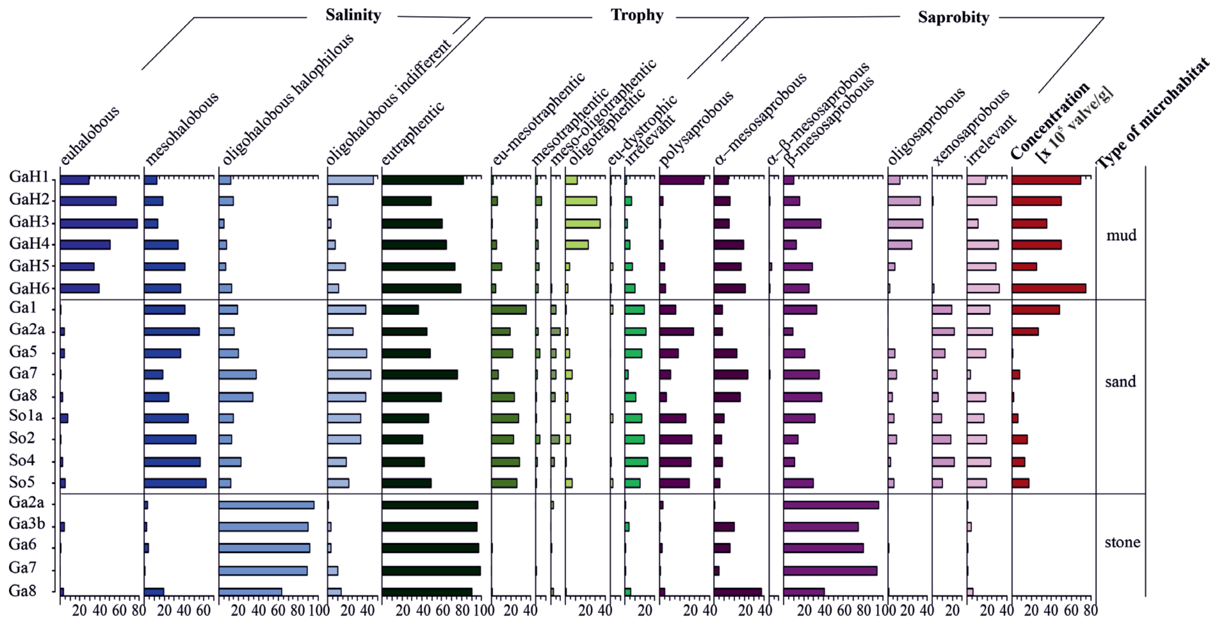

Figure 3

Percentage content of the diatom ecological groups in epilithon (stone), epipsammon (sand) and epipelon (mud)

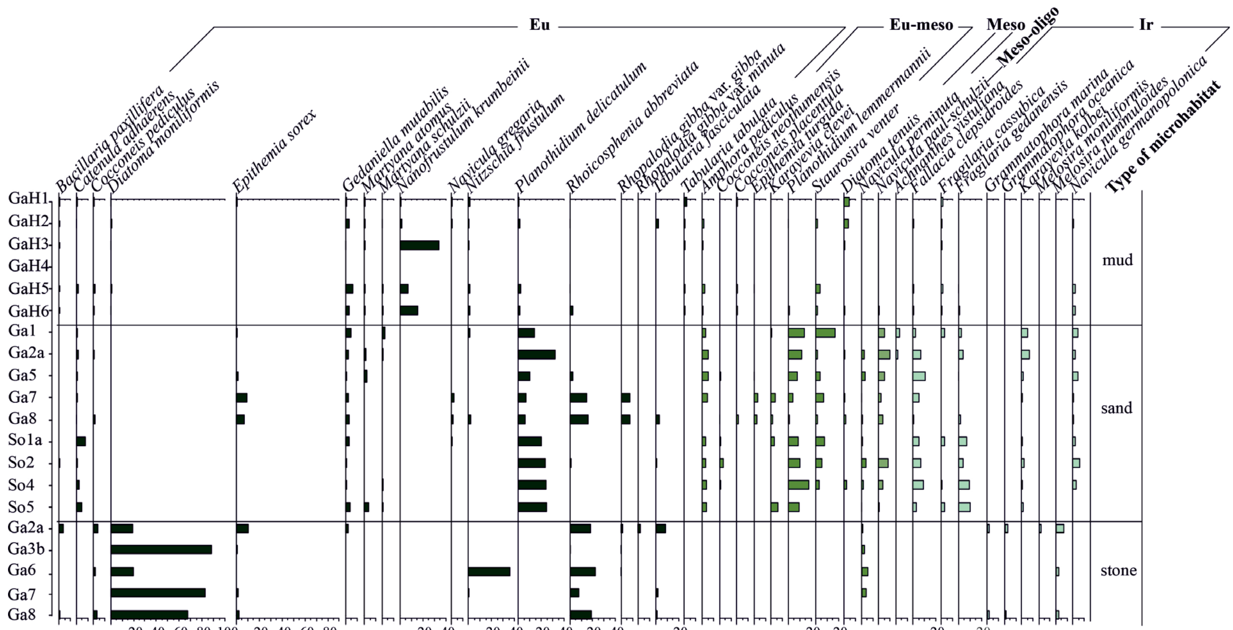

Figure 4

Frequency of the main diatom taxa in epilithon (stone), epipsammon (sand) and epipelon (mud)

β-mesosaprobionts, was frequently recorded. This species was particularly abundant in the marina in Gdynia (Ga1–2a) and in Sopot (So1a–2, So4–5). At these sites, a higher percentage of eu-mesotraphentic species was observed, i.e. *Amphora pediculus* (Kützing) Grunow, *Planothidium lemmermannii* (Hustedt) E.Morales and *Staurosira venter* (Ehrenberg) Cleve & Möller and the meso-oligotraphentic species *Navicula paul-schulzii* Witkowski & Lange-Bertalot. Among the brackish diatoms, *Fallacia clepsidroides* Witkowski, *Fragilaria cassubica* Witkowski & Lange-Bertalot, *F. gedanensis* Witkowski, *Navicula germanopolonica* occurred more frequently. A slightly different flora inhabits the sands in the Orłowo Cliff area (Ga7–8). In the epipsammon, oligohalobous halophilous and indifferent species, mainly those preferring waters rich in nutrients and organic matter, were more frequently observed. This group is represented by *C. placentula* Ehrenberg, *Epithemia sorex, E. turgida* (Ehrenberg) Kützing, *Rhoicosphaenia abbreviata*, and *Rhopalodia gibba* var. *gibba*. The highest concentration of valves in sandy sediments was recorded in the marina area (48 x 10^5 valves/g). Between sites Ga5 and Ga8, the concentration decreases (2 x 10^5 valves/g) and then increases in Sopot (17 x 10^5 valves/g; Fig. 3).

4.3. Epipelon

The epipelic assemblage found only in the Port of Gdynia (GH1–8) was dominated by eutraphentic (49–82%) and α- and β-mesosaprobic diatoms (10–30% and 10–35%, respectively; Fig. 3). The concentration of diatom valves is clearly higher in the port muds than in the sandy sediments of Gdynia and Sopot and ranges between 25 x 10^5 valves/g (GaH5) and 75 x 10^5 valves/g (GaH1). The marine species *Nanofrustulum krumbeinii* (Witkowski, Witak & Stachura) E. Morales has a higher frequency in the eutraphentic benthos, with a maximum at site GaH3 (34%; Fig. 4). It is accompanied by other marine diatoms, i.e. *Bacillaria paxillifera*, *Catenula adhaerens* and many brackish species, i.e. *Gedaniella mutabilis*, *Martyana schulzii* C. Brockmann, *M. atomus*, *Planothidium delicatulum, Tabularia fasciculata*. In the northern part of the port, a higher frequency of the freshwater species *Diatoma tenuis* is observed. Whereas in the southern part of the Port of Gdynia, the frequency of the freshwater species *Staurosira venter* increased.

4.4. Epiphyton

The epiphytic assemblage occurring at all sites in Gdynia and Sopot, except the port, is dominated by diatoms preferring nutrient-rich waters (70–98%) and tolerating large amounts of organic matter, i.e. α- and β-mesosaprobionts (33–91%, 7–62% respectively; Fig. 5). Between sites Ga1 and So1, the epiphytic assemblage is dominated by oligohalobous halophilous species, i.e. *Diatoma moniliformis*, *Epithemia sorex* and *Rhoicosphaenia abbreviata* (Fig. 6). Furthermore, the oligohalobous-indifferent species *Cocconeis pediculus* is also found there. The eu- and mesohalobous species, i.e. *Grammatophora marina*, *G. oceanica*, *Melosira moniliformis* and *M. nummuloides* are of lesser importance. At sites So2–5, mesohalobous species play a key role in diatom assemblages. This group is mostly represented by *Tabularia fasciculata* (35–67%), which is accompanied by *Bacillaria paxillifera* and *Navicula perminuta*.

5. Discussion

5.1. Diatoms versus microhabitats

Our results have shown significant differences in species spectra in relation to microhabitats. Changes in saline conditions caused by the inflow of river waters as well as anthropopressure had a significant impact on the species diversity of the diatom flora. The observed differences in individual diatom communities

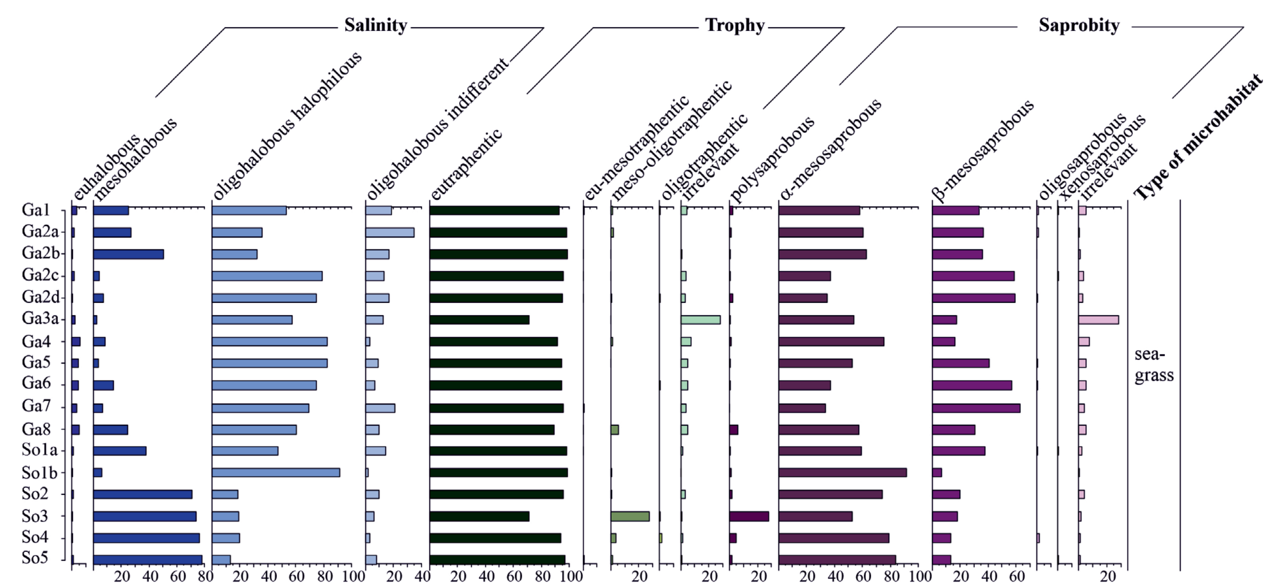

Figure 5

Percentage content of the diatom ecological groups in epiphyton (seagrass)

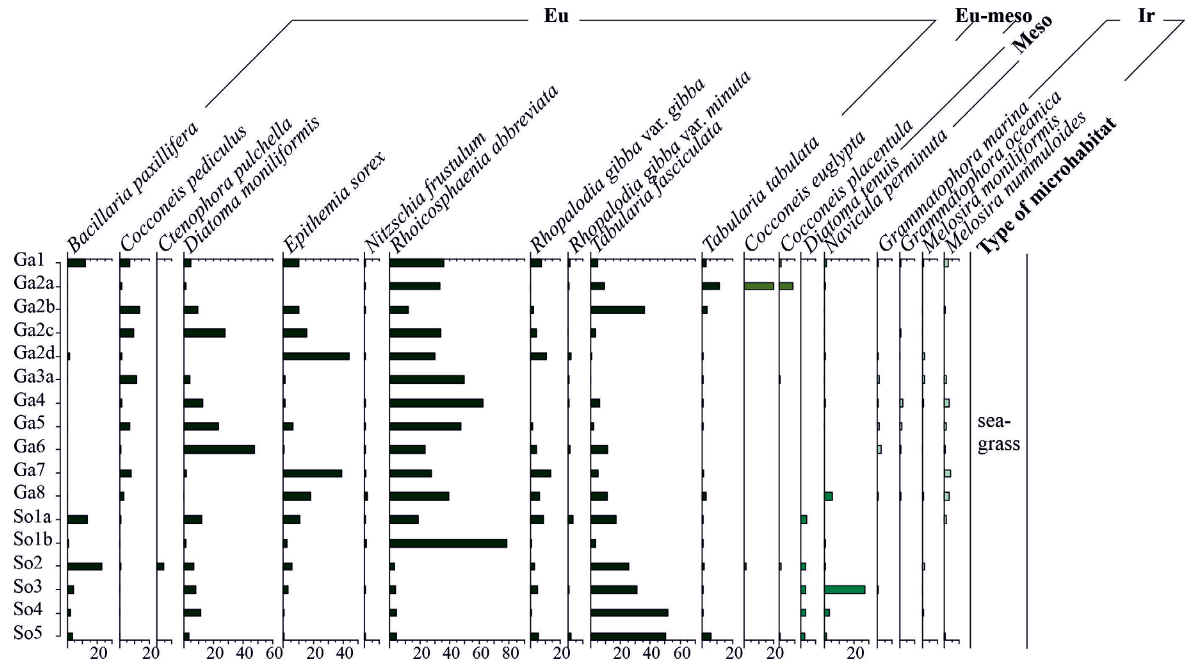

Figure 6

Frequency of the main diatom taxa in epiphyton (seagrass)

(epilithic, epipsammic, epipelic and epiphytic) allowed us to distinguish four groups: (1) species characteristic of one microhabitat, (2) species living in two types of microhabitats, (3) species observed in three microhabitats, and (4) species occurring in all types of microhabitats.

5.1.1. One microhabitat

Some diatom species were found in only one of the analyzed communities (epipsammon, epipelon, epiphyton). *Karayevia clevei* (Grunow) Bukhtiyarova and *Epithemia turgida* occurred only on sandy microhabitats in the study area (sites Ga1, Ga7–Ga8, So1a, So5 and Ga7–Ga8, respectively). The latter species is described as an epiphytic form (e.g. Snoeijs & Potapova 1995). *Cocconeis neothumensis* recorded in the study material with epipsammon (Snoeijs & Balashova 1998) was frequently observed at site So2. However, it was also observed in sandy muds of the Gulf of Gdańsk by Leśniewska & Witak (2008), Witak (2010) and Witak & Pędziński (2018). *Nanofrustulum krumbeinii* is a species recorded only in the epipelon of the coastal zone of the Gulf of Gdańsk (sites GaH1–GaH6). This small benthic diatom was also abundant in epilithic and epipsammic communities in the inner coastal zone of the Hel Peninsula between Jurata and Chałupy (Witak et al. 2020), as well as in muddy and sandy sediments of the Gulf of Gdańsk (Witak 2010; Leśniewska & Witak 2011; Pędziński &Witak 2019). Moreover, two species, *Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round (site So2) and *Cocconeis euglypta* Ehrenberg (sites Ga2a and So2), were recorded only in the epiphytic community. Both taxa were also abundant in the epiphyton of the coastal zone from the Hel Cape to Chałupy (Witak et al. 2020). Further, *C. euglypta* was often observed in the epilithic assemblage near Kuźnica.

5.1.2. Two microhabitats

Three groups were distinguished among the diatoms occurring in two microhabitats. The first group represented by *Rhopalodia gibba* var. *minuta*, *Grammatophora marina* and *Melosira moniliformis* is associated with epilithon and epiphyton. These species were more frequently observed in the epiphytic assemblage than in the epilithic community. This group also included *Grammatophora oceanica* and *Melosira nummuloides*, which were reported by Pliński & Witkowski (2011) and Witkowski (1994) in epiphytic assemblages of shallows in the Gulf of Gdańsk. The second group consisted of species connected with epipsammon and epipelon such as *Fragilaria cassubica*, *F. gedanensis* Witkowski, *Martyana schulzii* Brockmann, *M. atomus*. All mentioned taxa were reported by Snoeijs & Potapova (1995), Witkowski (1994), Witkowski et al. (2000) and Pliński & Witkowski (2011, 2013) in the epipsammic community. Furthermore, *Amphora pediculus*, *Catenula adhaerens*, *Navicula* *gregaria* Donkin, *Navicula paul-schulzii* and *Navicula germanopolonica*, which are commonly observed in muddy and sandy sediments of the Gulf of Gdańsk, were recorded in this group (Witak & Dunder 2007; Witak 2010, 2013; Leśniewska & Witak 2011; Witak & Pędziński 2018; Witak et al. 2020). The presence of *Planothidium delicatulum* and *Staurosira venter* is also characteristic for this community. Both species are abundant in sands and muds in different regions of the Gulf of Gdańsk and the Vistula Lagoon (Witak & Dunder 2007; Leśniewska & Witak 2008; Witak 2010; Witak & Pędziński 2018). However, they were also recorded on seagrasses and stones along the inner side of the Hel Peninsula (Witak et al. 2020). The species *Fallacia clepsidroides*, which was reported by Snoeijs & Potapova (1995) as an epipelic form, was also found in epipsammic and epipelic assemblages. Along the Hel Peninsula it was observed in epilithon and more often in epipsammon (Witak et al. 2020). The last group is related to the species *Tabularia tabulata* (C. Agardh) Snoeijs occurring in muddy sediments and seagrasses in the study area, which was observed in the largest numbers in the epiphyton (Ga1–Ga2b). This species was reported in the epiphytic community by Snoeijs (1993).

5.1.3. Three microhabitats

The species *Diatoma moniliformis* was observed in epilithon, epiphyton and epipelon. It reaches the highest frequency in the epilithon along the coastal zone of Gdynia (Ga2–Ga8). The species was most abundant in the epiphyton of the Hel Peninsula (Witak et al. 2020), where it was also observed in epilithon and epipsammon (Witak et al. 2020). *Diatoma tenuis*, defined by Snoeijs (1993) as an epiphytic species, was recorded in epipsammon, epipelon and epiphyton. The species occurred in the epilithic community in the inner side of the Hel Peninsula (Witak et al. 2020). The third group, represented by *Rhopalodia gibba* var. *gibba*, is associated with the epipsammic, epilithic and epiphytic community, but thrives most abundantly on seagrasses. The last group of diatoms, which was associated with epipsammon, epipelon and epilithon was marked by the presence of the species *Gedaniella mutabilis*, commonly observed in sandy and muddy sediments of Puck Bay and the Vistula Lagoon (Witak 2010, 2013; Witak & Pędziński 2018).

5.1.4. All microhabitats

Diatoms occurring in all types of microhabitats are represented by the species reported by Snoeijs (1993) in the epilithon (*Bacillaria paxillifera*, *Nitzschia frustulum*, *Navicula perminuta*) and epiphyton (*Cocconeis pediculus*, *Epithemia sorex*, *Tabularia fasciculata*). This group also includes *Rhoicosphaenia abbreviata* and *Tabularia fasciculata*, which were observed in all types of microhabitats along the Hel Peninsula (Witak et al. 2020). Several species, although occurring in all microhabitats, showed distinct preferences for one of them. *Rhoicosphaenia abbreviata* and *Tabularia fasciculata* predominate in the epiphytic community. The epilithic assemblage at site Ga6 shows an increase in the frequency of *Nitzschia frustulum*. This species is one of the main components of the diatom flora in all microhabitats of the inner Hel Peninsula (Witak et al. 2020). Moreover, epiphytic communities are characterized by a higher frequency of *Epithemia sorex*. In the epipsammic community, the most noteworthy sites are Ga7–8, where the frequency of *Epithemia sorex* and *Rhoicosphaenia abbreviata* increased. These species do not show a high affinity for the muddy microhabitat.

5.2. Diatoms versus location

5.2.1. Gdynia Port

The port of Gdynia is impacted by seawater of the Gulf of Gdańsk, which is well documented by the dominance of marine and brackish diatoms in the muddy sediments. Due to ship traffic and intensive port activity, the water column and bottom sediments contain a large number of organic pollutants. Diatom taphocoenoses in its north-western part (GaH1–2) are rich in polysaprobionts (≤ 44%) and β-mesosaprobionts (≤ 37%). Moreover, a higher frequency of the α-mesosaprobiont *Diatoma tenuis*, accompanied by *Tabularia fasciculata* and *T. tabulata*, is observed. The high level of organic matter in this area is related to the presence of a shipyard and the Baltic Container Terminal. The southern part of the Port of Gdynia (GaH4–6) is less contaminated with nutrients, which is indicated by the dominance of α- and β-mesosaprobionts, including frequently recorded *Nanofrustulum krumbeinii*. This species was commonly observed in the Gulf of Gdańsk (Leśniewska & Witak 2011; Pędziński & Witak 2019; Witak et al. 2020). The higher frequency of this benthic diatom is accompanied by an increase in the relative abundance of β-mesosaprobionts such as *Gedaniella mutabilis* and *Staurosira venter*. High organic pollution accumulated in the sediments of the Port of Gdynia is related to the composition of the sediment (Radke et al. 2013). The presence of a breakwater also has an unfavorable impact on the water state in the port. Despite its protective function, it has a negative impact on the environmental conditions due to the limitation of water exchange, which in turn does not allow the area to be cleaned of organic pollution with excessive amounts of nutrients. The relatively large depth of the Port of Gdynia contributes to the dominance of planktic anthropogenic species (*Cyclotella choctawhatcheeana*, *Thalassiosira levanderi*, *Stephanodiscus hantzschii*), which prefer high trophic requirements (Witak 2000, 2010; Leśniewska & Witak 2008, 2011; Witak & Pędziński 2018; Pędziński & Witak 2019).

5.2.2. Gdynia coastal zone

The inflow of water from the Kacza River has a significant impact on the salinity conditions in the this part of the coastal zone. The Kacza River is the second largest river flowing through the Tri-City (Augustowska et al. 1994). Between the marina (Ga1) and the Orłowo Headland (Ga8), brackish diatoms (*Fallacia clepsidroides*, *Planothidium delicatulum*) are gradually replaced by oligohalobous halophilous diatoms in epiphyton, epilithon and epipsammon, i.e. *Diatoma moniliformis*, *Epithemia sorex*, *Rhoicosphaenia abbreviata*. All the above-mentioned taxa were observed in different regions of the Gulf of Gdańsk (Witak 2010; Witak et al. 2020). As in the Port of Gdynia, the dominance of species with high trophic requirements is observed, including *Diatoma moniliformis*, *Epithemia sorex*, *Planothidium delicatulum*, *Rhoicosphaenia abbreviata*. Eutraphentic species constitute ≤ 98% in the epilithic and epiphytic community, while in the epipsammon they account for ≤ 76%. The high content of biogenic substances in this part of the coastal zone is related to urbanization. The higher frequency of polysaprobionts in the epipsammon (≤ 34%) in the northern part of the zone indicates a high content of organic matter in the vicinity of the marina (Ga1, Ga2a) and Seaside Boulevard (Ga5). Toward the south, the level of saprobity is lower, which is well documented by an increase in the frequency of α- and β-mesosaprobionts in the epilithic (≤ 47%, ≤ 95%), epiphytic (≤ 75%, ≤ 62%) and epipsammic community (≤ 25%, ≤ 38%).

5.2.3. Sopot coastal zone

The hydrological regime of the coastal zone in Sopot is influenced by saline waters of the Gulf of Gdańsk. This is evidenced by the dominance of eutraphentic mesohalobous, represented mostly by *Bacillaria paxillifera*, *Planothidium delicatulum* and *Tabularia fasciculata*. Their particularly high frequency is observed in epipsammon (≤ 62%) and epiphyton (≤ 77%). Other brackish diatoms, i.e. *Fallacia clepsidroides, Fragilaria cassubica, F. gedanensis, Navicula paul-schulzii* and *N. germanopolonica* were rarely observed. Abundance of oligohalobous halophilous taxa (*Diatoma moniliformis, Planothidium lemmermannii, Rhoicosphaenia abbreviata*) was recorded at sites So1 and So3–4, which is related to the influence of the Swelinia and Karlikowski streams. Moreover, representatives of oligohalobous indifferent diatoms (*Amphora pediculus*, *Diatoma moniliformis* and *Nitzschia frustulum*) were observed in taphocoenoses. These diatoms were also recorded at the mouth of nearby streams by Bogaczewicz-Adamczak et al. (2001) and Zgrundo & Bogaczewicz-Adamczak (2004). The presence of polysaprobionts and the abundance of α-mesosaprobionts, particularly in epiphytic assemblages, indicate a higher content of organic matter in the Sopot coastal zone, which is associated with high tourist traffic and close proximity to the urbanized zone.

6. Conclusions

The results of the diatom study in the coastal zone of the Gulf of Gdańsk, between Gdynia and Sopot, indicate the presence of a diverse flora belonging to epilithic, epipsammic, epipelic and epiphytic assemblages. Most of the identified benthic species occurred in two or three microhabitats:

- Epilithon and epiphyton were represented by *Rhopalodia gibba* var. *minuta*, *Grammatophora marina* and *Melosira moniliformis*. *Amphora pediculus*, *Catenula adhaerens*, *Fallacia clepsidroides*, *Fragilaria cassubica*, *F. gedanensis*, *F. schulzii*, *Martyana atomus*, *Navicula gregaria*, *N. paul-schulzii*, *N. germanopolonica*, *Planothidium delicatulum* and *Staurosira venter* were observed in the material collected from sandy and muddy sediments. *Tabularia tabulata* was observed in epipelon and epiphyton.

- The species *Diatoma moniliformis* was observed in epilithon, epiphyton and epipelon, while *D. tenuis* was associated with epipsammon, epipelon and epiphyton. The species *Rhopalodia gibba* var. *gibba* was associated with epipsammon, epilithon and epiphyton. Furthermore, epipsammon, epipelon and epilithon were represented by *Gedaniella mutabilis*.

However, considering the diatom–microhabitat relationships, two specific groups were distinguished:

- Epipsammon, epipelon and epiphyton were characterized by the presence of at least one species that was not observed in other communities. The species *Cocconeis neothumensis*, *Epithemia turgida* and *Karayevia clevei* are typical of epipsammon, while *Nanofrustulum krumbeinii* was observed only in epipelon. Furthermore, two species, *Ctenophora pulchella* and *Cocconeis euglypta*, are characteristic of the epiphyton.

- Some diatom species, i.e. *Bacillaria paxillifera*, *Cocconeis pediculus*, *Epithemia sorex*, *Navicula perminuta*, *Nitzschia frustulum*, *Rhoicosphaenia abbreviata* and *Tabularia fasciculata* were observed in all analyzed microhabitats, which means they do not have any preferences with respect to the type of substrate.

Based on the ecological preferences of the identified diatom flora, certain differences in the quality of water were observed in the Port of Gdynia and in the coastal zone of Gdynia and Sopot:

- The high frequency of α-mesosaprobionts dominated by *Bacillaria paxillifera*, *Rhoicosphaenia abbreviata* and *Tabularia fasciculata* may indicate the high level of organic matter in the study area. The highest frequency of these species was mostly observed in epiphyton and epilithon. The increased organic pollution in the waters of the Port of Gdynia and the marina is evidenced by the abundance of polysaprobiont taxa such as benthic *Navicula perminuta* present in the epipsammon, epilithon and epiphyton. A higher frequency of polysaprobionts was observed in the coastal zone of Sopot, due to the high tourist traffic and urbanization of the coastal zone.

- The high degree of eutrophication of the waters of the study area was evidenced by the abundance of species with high trophic requirements, represented by *Bacillaria paxillifera*, *Diatoma moniliformis*, *Epithemia sorex*, *Nanofrustulum krumbeinii*, *Nitzschia frustulum*, *Planothidium delicatulum*, *Rhoicosphaenia abbreviata* and *Tabularia fasciculata*.

- The change in salinity in the study area is related to the distance from the mouths of nearby rivers and streams. Due to the limited water dynamics associated with the breakwater, the area of the Port of Gdynia is dominated by marine species, of which *Nanofrustulum krumbeinii* predominates. The frequency of brackish species (*Navicula perminuta*, *Tabularia fasciculata*, *T. tabulata*, *Planothidium delicatulum*) increases in the vicinity of the marina in Gdynia and in the coastal zone of Sopot. Moreover, a higher frequency of freshwater species (*Amphora pediculus*, *Diatoma moniliformis*, *Epithemia sorex*, *Nitzschia frustulum*, *Rhoicosphaenia abbreviata*) is observed near the mouths of the Kacza River, and the Swelinia and Karlikowski streams.

Acknowledgements

This study was financed by the Department of Marine Geology, Institute of Oceanography, University of Gdańsk. The authors would like to thank anonymous reviewers for their comments that improved the manuscript. We thank Blanca Hinojosa, University of Huston-Downtown USA, for her help in collecting the material for the study.

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